

Active Brownian motion of an asymmetric rigid particle

Gulmammad Mammadov*

Department of Physics, Syracuse University, Syracuse, NY 13244-1130, USA

Abstract

Individual movements of a rod-like self-propelled particle on a flat substrate are quantified. Biological systems that fit into this description may be the Gram-negative delta-proteobacterium *Myxococcus xanthus*, Gram-negative bacterium *Escherichia coli*, and *Mitochondria*. There are also non-living analogues such as vibrated polar granulates and self-driven anisotropic colloidal particles. For that we study the Brownian motion of an asymmetric rod-like rigid particle self-propelled at a fixed speed along its long axis in two dimensions. The motion of such a particle in a uniform external potential field is also considered. The theoretical model presented here is anticipated to better describe individual cell motion as well as intracellular transport in 2D than previous models.

*Email: gmammado@syr.edu

1. INTRODUCTION

In classical physics the Brownian motion is the erratic motion of microscopic particles due to non-zero value of net stochastic forces at any given time exerted on them by atoms or molecules of the surrounding medium. Such microscopic particles don't play active role in the motion and their irreversible dissipation of energy is compensated by reversible thermal fluctuations as expressed in the fluctuation-dissipation theorem.

In contrast, if the particles have internal or external energy source leading to self-propulsion, their motion will have directional biasness. Such motion is referred to as the *active* Brownian motion. Some example subjects of active Brownian motion relevant to our study are self-driven colloidal particles, living microorganisms, and vibrated *Janus* particles [1–5]. These systems exhibit many interesting nonequilibrium effects understanding of which have been the research focus of many scientists in recent years.

In this context, a phenomenological model of active Brownian motion has been developed based on principle of energy take up, store and dissipation into kinetic degrees of freedom [6, 7]. Other research team, J. R. Howse *et al.*, experimentally studied active Brownian motion of spherical polystyrene particles that are self-propelled due to asymmetric surface activity [8]. They interpreted the data using an expression for the mean-squared displacement that takes into account rotational diffusion of the self-propulsion velocity. More recently motion of deformable self-propelled particles analytically has been studied assuming that the particles can deform from circular shape when the propagation velocity is increased [9]. It was shown that such a particle undergo a bifurcation from straight motion to a circular motion by increasing the propagation velocity. Also, Brownian dynamics of a microswimmer composed of three spheres which propels itself in a viscous fluid by spinning motion of the spheres under zero net torque has been studied [10]. Finally, in ref [2] dynamics of a Brownian circle swimmer has been studied when the driving force does not coincide with the propagation direction. It was hypothesized that when the self-propulsion force and the particle orientation are in line, the motion would be along a straight line just perturbed by random fluctuations.

In this paper, we present detailed study of the active Brownian motion of an asymmetric particle when the self-propulsion force and the particle orientation are in line. Unlike previous studies our approach takes into account the particle asymmetry.

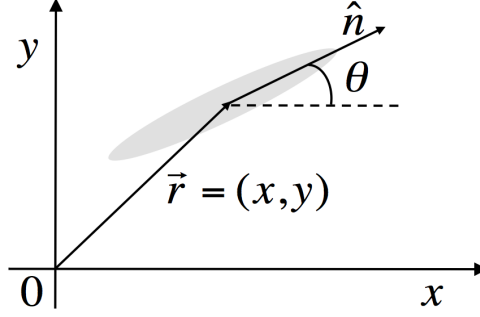


FIG. 1: The diagram shows an ellipsoidal rigid particle self-propelled along its long axis.

Collective behavior of such rods, which interact with each other through excluded volume, has been theoretically studied [11] and it was shown that the self-propulsion enhances the longitudinal diffusion coefficient. Our calculations, however, show that in the case of one rod both the longitudinal and the transverse diffusion coefficients are enhanced and assume the same value at long times.

The paper is organized as following: After introducing the model, we start by calculating the mean squared displacements and corresponding diffusion tensors for two cases: when a rod is self-propelled at constant speed and when such a self-propelled rod is in external constant potential field. The paper is concluded by the discussion of the results.

2. THE MODEL

The model consists of an ellipsoidal rigid particle that is self-propelled along its long axis and undergoing Brownian motion in two dimensions (see FIG. 1). Note that this model can be generalized to higher dimensions using the Pythagorean theorem.

At a given time t the rod can be described by the position vector of its center of mass $\mathbf{r}(t)$ and the angle $\theta(t)$ between the x axis of the *lab-frame* and the long axis of the rod. In this frame the self-propulsion speed, which is taken along the long axis of the rod, is given by $v\hat{\mathbf{n}}(t)$, where $\hat{\mathbf{n}}(t) \equiv (\cos\theta(t), \sin\theta(t))$ is a unit vector along the long axis of the rod. In the presence of external force \mathbf{F} and torque τ the dynamics of the rod is governed by the coupled Langevin equations, given by

$$\partial_t r_i = \Gamma_{ij}(\hat{\mathbf{n}})F_j + v\hat{n}_i(t) + \xi_i(t), \quad (1)$$

$$\partial_t \theta = \Gamma_R \tau + \xi_R(t), \quad (2)$$

where $i = x, y$ for $2D$ and Γ_{ij} , Γ_R are the mobilities relating velocity and angular velocity to force and torque, respectively. In the *body-frame* denoting the mobility along the long axis of the rod by Γ_{\parallel} and perpendicular by Γ_{\perp} , the mobility tensor in the lab-frame takes the following form

$$\Gamma_{ij}(\hat{n}) = \Gamma \delta_{ij} + \frac{\Delta \Gamma}{2} M_{ij}(\theta), \quad (3)$$

where $M_{ij}(\theta) = \begin{pmatrix} \cos 2\theta & \sin 2\theta \\ \sin 2\theta & -\cos 2\theta \end{pmatrix}$, $\Gamma = \frac{\Gamma_{\parallel} + \Gamma_{\perp}}{2}$, and $\Delta \Gamma = \Gamma_{\parallel} - \Gamma_{\perp}$. The rotational noise ξ_R is a Gaussian random variable with zero mean and variance

$$\langle \xi_R(t) \xi_R(t') \rangle = 2k_B T \Gamma_R \delta(t - t'), \quad (4)$$

whereas $\xi_x(t)$ and $\xi_y(t)$ are Gaussian at a fixed $\theta(t)$ with zero mean and variances depending on orientation at a given time

$$\langle \xi_i(t) \xi_j(t') \rangle_{\theta(t)} = 2k_B T \Gamma_{ij}(\theta(t)) \delta(t - t'), \quad (5)$$

where k_B is the Boltzmann constant and T is the effective temperature. The ensemble average is calculated using $\langle \dots \rangle = \frac{1}{2\pi} \int_0^{2\pi} \langle \dots \rangle_{\theta_0} d\theta_0$ where $\langle \dots \rangle_{\theta_0}$ indicates average both over $\xi_i(t)$ and $\xi_R(t)$ at a fixed initial angle.

The self-propulsion force doesn't induce torque, which in turn enables the rod to rotate freely about the axis passing through its center of mass and perpendicular to the plane of motion. This means that the angular displacements obey the Gaussian statistics with constant rotational diffusion coefficient. In the lab-frame the shape asymmetry of the rod makes the translational and rotational displacements coupled, which complicates the analytic examination of the motion. The Gaussianity of the angular displacements, however, simplifies the matter and leads to detailed analytic results.

3. SELF-PROPULSION AT CONSTANT SPEED

As we mentioned previously, to carry out the calculations analytically we shall set $\tau = 0$. Therefore in the absence of external torque integration of Eq. (2) gives $\Delta \theta(t) = \int_0^t \xi_R(t') dt'$. Then with the aid of Eq. (4) for the mean-squared angular displacement (the second moment)

we obtain

$$\langle [\Delta\theta(t)]^2 \rangle = \int_0^t \int_0^t \langle \xi_R(t') \xi_R(t'') \rangle dt' dt'' = 2D_R t.$$

Subsequently the noise averages of the sinusoidal functions will be evaluated using the following identity [13]:

$$\langle e^{i[s_1 \Delta\theta(t_1) + s_2 \Delta\theta(t_2)]} \rangle_{\theta_0} = e^{-D_R[s_1^2 t_1 + s_2^2 t_2 + 2s_1 s_2 \min(t_1, t_2)]}, \quad (6)$$

where $D_R = k_B T \Gamma_R$ is the rotational diffusion coefficient.

Following the derivation of Ref. [14] in the absence of external force \mathbf{F} one can integrate Eq. (1) with respect to time and use Eq. (A6) to calculate the ensemble average of the sinusoidal functions. Then for the mean displacement one obtains

$$\langle \Delta \mathbf{r} \rangle_{\theta_0} = v \tau_1 (\cos \theta_0, \sin \theta_0), \quad (7)$$

where $\tau_n = \frac{1 - e^{-n D_R t}}{n D_R}$ and $\tau_R = 1/2 D_R$ is the rotational time required for one radian diffusion.

Finally, using Eq. (7) for the magnitude of the mean displacement of the rod one has

$$|\langle \Delta \mathbf{r} \rangle_{\theta_0}| = [\langle \Delta x \rangle_{\theta_0}^2 + \langle \Delta y \rangle_{\theta_0}^2]^{\frac{1}{2}} = 2v \tau_R [1 - e^{-\frac{t}{2\tau_R}}]. \quad (8)$$

To find the mean-squared displacement tensor resulting from the integration of Eq. (1) with $\mathbf{F} = 0$, we note that on averaging over the noise, cross terms such as $\langle \xi_i(t_1) n_j(t_2) \rangle$ vanish since they are first order in the noise. After doing so, in the expression for the mean-squared displacement tensor we are left with only two terms

$$\begin{aligned} \langle \Delta x_i(t) \Delta x_j(t) \rangle_{\theta_0} &= \int_0^t dt_1 \int_0^t dt_2 \langle \xi_i(t_1) \xi_j(t_2) \rangle_{\theta_0} \\ &+ v^2 \int_0^t dt_1 \int_0^t dt_2 \langle n_i(t_1) n_j(t_2) \rangle_{\theta_0}. \end{aligned} \quad (9)$$

The first term in Eq. (9) has been calculated in ref. [14] and the second term is given by Eq. (A7). If we put them together, for the mean-squared displacement tensor at a fixed initial orientation we obtain

$$\begin{aligned} \langle \Delta x_i \Delta x_j \rangle_{\theta_0} &= [2Dt + 2\tau_R v^2 (t - \tau_1)] \delta_{ij} \\ &+ [\Delta D \tau_4 + \frac{2\tau_R v^2}{3} (\tau_1 - \tau_4)] M_{ij}(\theta_0), \end{aligned} \quad (10)$$

and the mean-squared displacement

$$\langle \Delta \mathbf{r}^2 \rangle = 4Dt + 4\tau_R v^2 [t - 2\tau_R(1 - e^{-t/2\tau_R})], \quad (11)$$

with $D = k_B T \Gamma$ and $\Delta D = k_B T \Delta \Gamma$. For the displacement diffusion tensor of an active rod Eq. (10) yields

$$\begin{aligned} D_{ij}(t, \theta_0) &= \frac{\langle \Delta x_i \Delta x_j \rangle_{\theta_0}}{2t} = [D_S - \tau_R v^2 \frac{\tau_1}{t}] \delta_{ij} \\ &+ \Delta D \frac{\tau_4}{2t} [1 + \frac{2\tau_R v^2}{3\Delta D} \frac{\tau_1 - \tau_4}{\tau_4}] M_{ij}(\theta_0), \end{aligned} \quad (12)$$

where $D_S = D + \tau_R v^2$. Averaging Eq. (12) over the initial angle, θ_0 , yields a time-dependent displacement diffusion tensor,

$$D_{ij}(t) = \frac{1}{2\pi} \int_0^{2\pi} d\theta_0 D_{ij}(t, \theta_0) = [D_S - \tau_R v^2 \frac{\tau_1}{t}] \delta_{ij}. \quad (13)$$

This shows that the system of non-interacting self-propelled rods is no longer diffusive as the displacement diffusion tensor is time dependent. However, in all cases the time dependence becomes negligible for $t \gg \tau_R$, and as t tends to infinity unlike the *passive* ellipsoidal rigid particle case, for the self-propelled ellipsoid the single long-time diffusion coefficient is enhanced according to

$$D_{ij}(t) \rightarrow D_S \delta_{ij}. \quad (14)$$

When $t \gg \tau_R$ the directional memory is lost and the rod behaves as a perfect spherical Brownian particle with enhanced diffusion coefficient.

On the other hand, when $t \ll \tau_R$ the diffusion tensor and the mean-squared displacement are give by $D_{ij}(t) \simeq [D + \frac{v^2 t}{4}] \delta_{ij}$ and $\langle \Delta \mathbf{r}^2 \rangle \simeq 4Dt + v^2 t^2$, respectively, indicating ballistic behavior at short times.

4. SELF-PROPULSION IN EXTERNAL CONSTANT FORCE POTENTIAL FIELD

In the previous section we studied the active Brownian motion of a rigid rod in the absence of external field and torque. Here we discuss the motion under the infulance of external constant force. As in the previous case we assume the rod is constrained to move

in a plane. An example of such a system may be active colloidal suspension of asymmetric particles under gravity.

Without loosing any generality, we can always rotate the coordinate system (lab-frame) such that the external force is along the x axis, $\mathbf{F} = F\hat{x}$. Then using Eq. (3) from Eq. (1) we can write

$$\begin{aligned}\Delta x(t) = F\Gamma t + \frac{1}{2}F\Delta\Gamma \int_0^t \cos 2\theta dt' \\ + \int_0^t \xi_x dt' + v \int_0^t \cos \theta dt',\end{aligned}\tag{15}$$

$$\Delta y(t) = \frac{1}{2}F\Delta\Gamma \int_0^t \sin 2\theta dt' + \int_0^t \xi_y dt' + v \int_0^t \sin \theta dt',\tag{16}$$

with averages given by

$$\begin{aligned}\langle \Delta x \rangle_{\theta_0} &= F\Gamma t + v\tau_1 \cos \theta_0 + \frac{1}{2}F\Delta\Gamma\tau_4 \cos 2\theta_0, \\ \langle \Delta y \rangle_{\theta_0} &= v\tau_1 \sin \theta_0 + \frac{1}{2}F\Delta\Gamma\tau_4 \sin 2\theta_0.\end{aligned}\tag{17}$$

The averages of the mean-squared displacements along the x and y axes are given by

$$\begin{aligned}\langle \Delta x^2 \rangle_{\theta_0} &= \frac{\tau_R}{24}F^2\Delta\Gamma^2[3(t - \tau_4) + (\tau_4 - \tau_{16}) \cos 4\theta_0] \\ &+ \Delta D\tau_4 \cos 2\theta_0 + F^2\Gamma\Delta\Gamma t\tau_4 \cos 2\theta_0 + 2vF\Gamma t\tau_1 \cos \theta_0 \\ &+ 2Dt + F^2\Gamma^2 t^2 + \frac{2}{3}\tau_R v^2[3(t - \tau_1) + (\tau_1 - \tau_4) \cos 2\theta_0] \\ &+ \frac{1}{120}\tau_R v F\Delta\Gamma[40(4\tau_1 - 3te^{-D_R t} - \tau_4) \cos \theta_0 \\ &\quad + 3(5\tau_1 + 8\tau_4 - 13\tau_9) \cos 3\theta_0],\end{aligned}\tag{18}$$

$$\begin{aligned}\langle \Delta y^2 \rangle_{\theta_0} &= \frac{\tau_R}{24}F^2\Delta\Gamma^2[3(t - \tau_4) - (\tau_4 - \tau_{16}) \cos 4\theta_0] \\ &- \Delta D\tau_4 \cos 2\theta_0 + \frac{2}{3}\tau_R v^2[3(t - \tau_1) - (\tau_1 - \tau_4) \cos 2\theta_0] \\ &+ \frac{1}{120}\tau_R v F\Delta\Gamma[40(4\tau_1 - 3te^{-D_R t} - \tau_4) \cos \theta_0 \\ &\quad - 3(5\tau_1 + 8\tau_4 - 13\tau_9) \cos 3\theta_0] + 2Dt,\end{aligned}\tag{19}$$

and the average of the cross-correlation between displacements along the x and y axes is

$$\begin{aligned}\langle \Delta x \Delta y \rangle_{\theta_0} &= \frac{\tau_R}{24} F^2 \Delta \Gamma^2 (\tau_4 - \tau_{16}) \sin 4\theta_0 + v F \Gamma t \tau_1 \times \\ &\sin \theta_0 + \frac{1}{2} F^2 \Gamma \Delta \Gamma t \tau_4 \sin 2\theta_0 + \frac{2}{3} \tau_R v^2 (\tau_1 - \tau_4) \sin 2\theta_0 \\ &+ \frac{1}{40} \tau_R v F \Delta \Gamma (5\tau_1 + 8\tau_4 - 13\tau_9) \sin 3\theta_0,\end{aligned}\tag{20}$$

In our calculations we took into account that the terms odd in the noise average to zero. Then the mean-squared displacement is

$$\begin{aligned}\langle \Delta \mathbf{r}^2 \rangle &= \frac{1}{2\pi} \int_0^{2\pi} d\theta_0 \frac{\langle \Delta y^2 \rangle_{\theta_0} + \langle \Delta x^2 \rangle_{\theta_0}}{2t} \\ &= 4Dt + 4\tau_R v^2 (t - \tau_1) + F^2 \Gamma^2 t^2 \\ &\quad + \frac{1}{4} F^2 \Delta \Gamma^2 \tau_R (t - \tau_4),\end{aligned}\tag{21}$$

and the long time $t \gg \tau_R$ diffusion tensor averaged over the initial angle, θ_0 , yields the following expression

$$D_{ij}(t) = \frac{1}{2\pi} \int_0^{2\pi} d\theta_0 \frac{\langle \Delta x_i \Delta x_j \rangle_{\theta_0}}{2t} = D_{SF} \delta_{ij}\tag{22}$$

with

$$\begin{aligned}D_{SF} &= D + \tau_R v^2 + v F \Delta \Gamma \tau_R \\ &\quad + \frac{1}{16} F^2 \Delta \Gamma^2 \tau_R + \frac{1}{4} F^2 \Gamma^2 t.\end{aligned}\tag{23}$$

Self-propulsion vs. external potential field - We saw that for the self-propelled particle the long time single diffusion coefficient is enhanced according to $D_S = D + \tau_R v^2$. This enhancement is similar to that of a non self-propelled ellipsoid due to external constant potential field ($D_F = D + \tau_R |\mathbf{F}|^2 \Delta \Gamma^2 / 16$ where $|\mathbf{F}|$ is the force magnitude of the external potential field [15]) since both of them are proportional to the square of the force magnitude. However, the latter explicitly depends on the asymmetry of the particle, $\Delta \Gamma$, but the former does not. The origin of this discrepancy may be apparent from the fact that our model assumes that in addition to the external constant force the rod has a fixed speed v directed

along its long axis at all times while the former model assumes the rod feels only an external constant force \mathbf{F} at all times. Therefore similar to the hydrodynamic drag force, the external potential field brings in the friction factor between the two situations.

Also, a clear difference between the two situations is easily understood by neglecting the noise and hence considering a deterministic description. Then one can immediately calculate the velocity and displacement in the lab frame as functions of time and the initial angle, θ_0 , for given initial conditions. In the absence of external potential field we have zero mean displacement and zero velocity when averaging over θ_0 . However, in the presence of external potential field one obtains a mean velocity ΓF_x in the x direction and ΓF_y in the y direction with corresponding mean displacements.

5. DISCUSSION

In writing down the Eqs. (1) and (2) we have dropped the inertial terms assuming the motion is overdamped, that is, the viscous terms dominate the inertial ones. If we had kept those terms, they would have generated homogenous part of the solutions which exponentially decay with the characteristic *relaxation times*, $m \times \Gamma_{ij}$ for translational and $I \times \Gamma_R$ for rotational motion. Here m is the mass and I is the moment of inertia about the z axis passing through the center of mass of the rod. Our results are, therefore, not valid in time intervals comparable to the relaxation times given the fact that recently developed experimentation technics, namely, use of the Photonic Force Microscopy allows high precision measurements in such small time intervals [12].

Mean displacement - Eq. (8) has limiting forms of $|\langle \Delta \mathbf{r} \rangle_{\theta_0}| = 2v\tau_R$ for $t \gg \tau_R$ suggesting that at very long times the self-propelled rod must behave as a spherical Brownian particle in the region centered $2v\tau_R$ far from its initial position and $|\langle \Delta \mathbf{r} \rangle_{\theta_0}| = vt$ for $t \ll \tau_R$. The latter is intuitive since at early times the motion is anisotropic which is not the case for the long time result. To give a full physical meaning to these results, we contrast the cases when the self-propulsion (SP) is ‘turned on’ and ‘off’. First thing to note about these two situations is that both of them have the same rotational time, τ_R , since the net torque is zero in both cases. Using this, we can picture what the rod would do before and after the crossover has occurred when the SP is on and when it is off: (i) before the crossover ($t < \tau_R$), short time anisotropy gets contribution from SP which causes the rod move faster

in a particular direction than when SP is turned off. Therefore in the anisotropic regime the rod displaces more due to SP than when SP is turned off, (ii) after the crossover has occurred ($t > \tau_R$), in both cases the rod starts performing isotropic diffusion about the position that it has arrived during the time while $t < \tau_R$. Therefore $2v\tau_R$ is the mean distance between the *centers of isotropic diffusion* domains of non self-propelled and self-propelled rods.

Note that if we average over the initial orientation, components of the mean displacement are zero and so is the mean displacement. This is not in contradiction with what we have above. Averaging over the initial angle is equivalent to averaging over the number of non-interacting self-propelled rods that started up from the same point in isotropic manner. At long times, the centers of isotropic diffusion for these rods are distributed isotropically about the starting point and hence have zero mean displacement. From this point of view, we average the diffusion tensor over the initial orientation to analyze transient behavior of diffusion in the system of non-interacting such rods.

A particle undergoing classical Brownian motion takes the same amount of time for going from a given initial point to a final point and coming back. For our model this is not the case: The domain of isotropic motion is centered $2v\tau_R$ far from an arbitrary starting point implying that a particle would need more time (equivalently less probability) for coming back. In fact, it has been observed that when the *pigment granules* are spreading out from nucleus of the cell, they go straight through *actin filament* intersections until they get to the end of the filament, but if they need to return to the nucleus, *cargos* often switch at actin filament intersections hence taking relatively longer time to come back [17]. This is in accordance with the prediction of the model presented here.

Mean-squared displacement - In Eq. (11) the second term is exactly the same as the one in refs [18–20] obtained for the *persistent random walk* [21] with persistence time $P = 2\tau_R$ and the weak noise limit of the expression obtained from a model of Brownian particles which are pumped with energy by means of a non-linear friction function (upon setting $\tau_R = v_0^2/4D$) in refs [6, 7], while the first term is the contribution due to *classical Brownian motion*. This is similar to that of the Levy-walk superdiffusive motion which can be decomposed into thermal orientation fluctuations and an active motion of the rods with a constant velocity along their long axis [31].

It is known that at short times the cell appears to persist at the direction of motion but at long times the pattern of movement is similar to the classical Brownian motion [22]. Because

of this, the persistent random walk model have been used to quantify cell migrations [23–30]. The results presented here suggest that by including contribution due to the classical Brownian motion as in Eq. (11) one can describe individual cell movements on a plane substrate more accurately than it has been using the persistent random walk model.

Recently, an experiment has been carried out by Jonathan R. Howse, *et al.* who studied the motion of polystyrene spheres with a diameter of $1.62\ \mu\text{m}$ immersed in hydrogen peroxide and half-coated with platinum [8]. Due to the local osmotic pressure gradient created by the asymmetric chemical reaction such spheres were propelled. They were able to fit the experimental data only with the short- and long-time limits of the expression for their model, which is the same as Eq. (11) if we replace τ_R with $\tau_R/4$. But if we consider the displacement components along the x and y axes separately, then immediately we see a major difference between these two cases which has been hidden in the expressions for the mean-squared displacements. The first model consists of a self-propelled sphere whose direction of motion is subject to diffusion and hence no expression could contain shape asymmetry as it is zero. In contrast, our model contains shape asymmetry, ΔD , which makes it distinct from any previously studied model when considering the x and y components of quantities of our interest, such as the mean-squared displacement. We are able to recover all previously obtained results upon setting $\Delta D = 0$ in our calculations.

In summery, here we present a simple model to describe the individual movements of rod-like living microorganisms on a plain. For that we studied the Brownian motion of an asymmetric rigid particle self-propelled at a fixed speed v along its long axis in two dimensions. The results for the case when such a particle is in external potential field are also presented. Some relevant biological systems are rod like living microorganisms such as the Gram-negative delta-proteobacterium *Myxococcus xanthus*, Gram-negative bacterium *Escherichia coli* and *Mitochondria*. Non-living self-propelled systems which resemble our model may be a polar rod on a vibrating substrate [1], self-driven anisotropic colloidal particles and catalytically driven *nanorods* [2, 3]. These results are expected to better quantify motion of such systems over the entire range of time.

Acknowledgments

I would like to thank M. Cristina Marchetti who posed the problem and supervised me

during the earlier calculations. I also wish to thank Natsuhiko Yoshinaga, Arshad Kudrolli, Eric Lauga, and Clare Yu for helpful discussion of the work during the poster session of the I2CAM Workshop in Syracuse.

Appendix A

Here all averages $\langle \dots \rangle$ are taken at a fixed initial angle, θ_0 , and $\theta_1 \equiv \theta(t_1)$ and $\theta_2 \equiv \theta(t_2)$.

We start by writing

$$\langle n_i(t_1)n_j(t_2) \rangle = \begin{pmatrix} \langle \cos \theta_1 \cos \theta_2 \rangle & \langle \cos \theta_1 \sin \theta_2 \rangle \\ \langle \sin \theta_1 \cos \theta_2 \rangle & \langle \sin \theta_1 \sin \theta_2 \rangle \end{pmatrix}, \quad (\text{A1})$$

and

$$\begin{aligned} \cos \theta_1 \cos \theta_2 &= \frac{1}{2} [\cos(\theta_1 - \theta_2) + \cos(\theta_1 + \theta_2)], \\ \cos \theta_1 \sin \theta_2 &= \frac{1}{2} [\sin(\theta_1 + \theta_2) - \sin(\theta_1 - \theta_2)], \\ \sin \theta_1 \cos \theta_2 &= \frac{1}{2} [\sin(\theta_1 - \theta_2) + \sin(\theta_1 + \theta_2)], \\ \sin \theta_1 \sin \theta_2 &= \frac{1}{2} [\cos(\theta_1 - \theta_2) - \cos(\theta_1 + \theta_2)]. \end{aligned} \quad (\text{A2})$$

To calculate the averages we use Eq. (9) and the fact that $\cos \theta = \Re e^{i\theta}$ and $\sin \theta = \Im e^{i\theta}$ where \Re and \Im stand for the real and imaginary parts respectively. Then

$$\begin{aligned} 2\langle \cos \theta(t_1) \cos \theta(t_2) \rangle &= e^{-D_R[t_1+t_2-2\min(t_1,t_2)]} \\ &\quad + \cos 2\theta_0 e^{-D_R[t_1+t_2+2\min(t_1,t_2)]}, \\ 2\langle \sin \theta(t_1) \sin \theta(t_2) \rangle &= e^{-D_R[t_1+t_2-2\min(t_1,t_2)]} \\ &\quad - \cos 2\theta_0 e^{-D_R[t_1+t_2+2\min(t_1,t_2)]}, \\ 2\langle \cos \theta(t_1) \sin \theta(t_2) \rangle &= \sin 2\theta_0 e^{-D_R[t_1+t_2+2\min(t_1,t_2)]}, \\ 2\langle \sin \theta(t_1) \cos \theta(t_2) \rangle &= \sin 2\theta_0 e^{-D_R[t_1+t_2+2\min(t_1,t_2)]}. \end{aligned} \quad (\text{A3})$$

If we put Eq. (A3) into Eq. (A1), we obtain

$$2\langle n_i(t_1)n_j(t_2)\rangle_{\theta_0} = \delta_{ij}e^{-D_R[t_1+t_2-2\min(t_1,t_2)]} + M_{ij}(\theta_0)e^{-D_R[t_1+t_2+2\min(t_1,t_2)]} \quad (\text{A4})$$

Now we need to integrate Eq. (A4) twice. To do that we use the following formulae

$$\int_0^t dt_1 \int_0^t dt_2 \dots = \underbrace{\int_0^t dt_1 \int_0^{t_1} dt_2 \dots}_{t_1 > t_2} + \underbrace{\int_0^t dt_2 \int_0^{t_2} dt_1 \dots}_{t_1 < t_2}, \quad (\text{A5})$$

which can easily be proved using geometrical considerations. Then we have

$$\begin{aligned} & \int_0^t dt_1 \int_0^t dt_2 e^{-D_R[t_1+t_2+2\min(t_1,t_2)]} \\ &= 2 \int_0^t dt_1 \int_0^{t_1} dt_2 e^{-D_R[t_1+3t_2]} = \frac{4\tau_R}{3}[\tau_1(t) - \tau_4(t)], \\ & \int_0^t dt_1 \int_0^t dt_2 e^{-D_R[t_1+t_2-2\min(t_1,t_2)]} \\ &= 2 \int_0^t dt_1 \int_0^{t_1} dt_2 e^{-D_R[t_1-t_2]} = 4\tau_R[t - \tau_1(t)]. \end{aligned} \quad (\text{A6})$$

Finally, if we put Eqs. (A4), and (A6) together, we obtain

$$\begin{aligned} & v^2 \int_0^t dt_1 \int_0^t dt_2 \langle n_i(t_1)n_j(t_2)\rangle_{\theta_0} \\ &= 2\tau_R v^2[t - \tau_1]\delta_{ij} + \frac{2}{3}\tau_R v^2[\tau_1 - \tau_4]M_{ij}(\theta_0). \end{aligned} \quad (\text{A7})$$

-
- [1] Arshad Kudrolli, Geoffroy Lumay, Dmitri Volfson, and Lev S. Tsimring, *Swarming and Swirling in Self-Propelled Polar Granular Rods*, Phys. Rev. Lett. **100**, 058001 (2008).
 - [2] Sven van Teeffelen and Hartmut Löwen, *Dynamics of a Brownian circle swimmer*, Phys. Rev. E **78**, 020101(R)(2008).
 - [3] N. Bala Saidulu and K. L. Sebastian, *Interfacial tension model for catalytically driven nanorods*, J. Chem. Phys. **128**, 074708 (2008).
 - [4] Andreas Walther and Axel H. E. Müller, *Janus particles*, Soft Matter **4**, 663 - 668(2008).
 - [5] R. Golestanian, T. B. Liverpool and A. Ajdari, *Designing phoretic micro- and nano-swimmers*, New J. Phys. **9**, 126 (2007).

- [6] U. Erdman, W. Ebeling, L. Schimansky-Geier, and F. Schweitzer *Brownian Particles far from Equilibrium*, Euro. Phys. J., **15**:105-113(2000).
- [7] W. Ebeling and I. M. Sokolov, *Statistical Thermodynamics and Stochastic Theory of Nonequilibrium Systems* (World Scientific, London, 2005).
- [8] Jonathan R. Howse, Richard A. L. Jones, Anthony J. Ryan, Tim Gough, Reza Vafabakhsh, and Ramin Golestanian, *Self-Motile Colloidal Particles: From Directed Propulsion to Random Walk*, Phys. Rev. Lett. **99**, 048102(2007).
- [9] Takao Ohta and Takahiro Ohkuma, *Deformable self-propelled particles*, Phys. Rev. Lett. **102**, 154101 (2009).
- [10] Vladimir Lobaskin, Dmitry Lobaskin and Igor Kulic, *Brownian dynamics of a microswimmer*, Eur. Phys. J. Special Topics **157**, 149-156 (2008).
- [11] A. Baskaran and M. C. Marchetti, *Enhanced diffusion and ordering of self propelled rods*, Phys. Rev. Lett. **101**, 268101 (2008).
- [12] B. Luki, et al. *Direct Observation of Nondiffusive Motion of a Brownian Particle*, Phys. Rev. Lett. **95**, 160601 (2005).
- [13] K. Schulten, I. Kosztin, *Lectures in Theoretical Biophysics*, University of Illinois at Urbana - Champaign, 2000.
- [14] Y. Han, et al. *Brownian Motion of an Ellipsoid*, Science **314**, 626 (2006).
- [15] R. Grima and S. N. Yaliraki, *Brownian motion of an asymmetrical particle in a potential field*, J. Chem. Phys. **127**, 8 (2007). To be rigorous, non-Gaussianity manifest itself in the nonzero values of fourth- or higher-order cumulants, see ref. [14].
- [16] S. Prager, *Interaction of Rotational and Translational Diffusion*, J. Chem. Phys. **23**, 2404 (1955).
- [17] Joseph Snider, Francis Lin, Neda Zahedi, Vladimir Rodionov, Clare C. Yu, and Steven P. Gross, *Intracellular actin-based transport: How far you go depends on how often you switch*, Proc. Nat. Acad. Sci. USA, Vol. 101, No. 36, pp. 13204-13209 (September, 2004).
- [18] G. A. Dunn, *Characterising a kinesis response: time averaged measures of cell speed and directional persistence*, Agents Actions (Suppl) **12**:14-33(1983).
- [19] H. G. Othmer, S. R. Dunbar and W. Alt, *Models of dispersal in biological systems*, J. Math. Biol., **26**:263-298(1988).
- [20] C. L. Stokes, D. A. Lauffenburger and S. K. Williams, *Migration of individual microvessel*

- endothelial cells: stochastic model and parameter measurement*, J. Cell Sci., **99**:419-30(1991).
- [21] Randall D. Kamien has a remarkable derivation for the mean-squared displacement of a persistent random walk using the differential geometry in *The geometry of soft materials: a primer*, Rev. Mod. Phys, **74**, 953 - 971 (2002).
- [22] W. Mark Saltzman, *Tissue engineering*, (Oxford University Press, 2004).
- [23] S. Kouvroukoglou, K. C. Dee, R. Bizios, L. V. McIntire, and K. Zygourakis, *Endothelial cell migration on surfaces modified with immobilized adhesive peptides*, Biomaterials, **21**:1725-1733(2000).
- [24] R. B. Dickinson, J. B. McCarthy and R. T. Tranquillo, *Quantitative characterization of cell invasion in vitro: formulation and validation of a mathematical model of the collagen gel invasion assay*, Ann. Biomed. Eng., **21**:679-697(1993).
- [25] W. M. Saltzman, P. Parsons-Wingerter, K. W. Leong and L. Shin, *Fibroblast and hepatocyte behavior on synthetic polymer surfaces*, J. Biomed. Mater. Res., **25**:741-759(1991).
- [26] P. A. Dimilla, J. A. Quinn, S. M. Albelda, and D. A. Lauffenburger, *Measurement of individual cell migration parameters for human tissue cells*, AIChE J., **38**:1092-1104(1992).
- [27] J. E. Glasgow, B. E. Farrell, E. S. Fisher, D. A. Lauffenburger, and R. P. Daniele, *The motile response of alveolar macrophages. An experimental study using single-cell and cell population approaches*, Am. Rev. Respir. Dis., **139**:320-329(1989).
- [28] J. Tan, H. Shen and W. M. Saltzman, *Micron-scale positioning of features influences the rate of polymorphonuclear leukocyte migration*, Biophys. J., **81**:2569-2579(2001).
- [29] Alexis Petak and Stephen D Waldman, *Seeing Tissue as a 'phase of matter': exploring statistical mechanics for the cell*, Phys. Biol., **5**(1):16007(2008).
- [30] John P. Fisher, Antonios G. Mikos and Joseph D. Bronzino, *Tissue Engineering* (Tylor & Francis Group, 2007).
- [31] P. Dhar, Th. M. Fischer, Y. Wang, T. E. Mallouk, W. F. Paxton, and A. Sen, *Autonomously Moving Nanorods at a Viscous Interface*, Nano Lett. **6**(1), 66-72 (2006).